

ANNALS of CARNEGIE MUSEUM

CARNEGIE MUSEUM OF NATURAL HISTORY

4400 FORBES AVENUE • PITTSBURGH, PENNSYLVANIA 15213

VOLUME 47

28 JUNE 1978

ARTICLE 11

A NEW SPECIES OF AQUATIC *ANOLIS* (SAURIA, IGUANIDAE) FROM HISPANIOLA

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ABSTRACT

A new species of Alpha section aquatic *Anolis* is described from northern Haiti on the West Indian island of Hispaniola. Comparisons of the new species with its Beta section mainland aquatic relatives, as well as with the Cuban Alpha section *A. vermiculatus*, are made. The habitat and ecology of the type-locality are discussed in detail, and the coloration of the dewlap and its significance are postulated.

INTRODUCTION

Schwartz and Thomas (1975) listed 30 native and two introduced species of the iguanid lizard genus *Anolis* from the Antillean island of Hispaniola. One additional species has been described since 1975. Of these species, one (*A. brevirostris* Bocourt) is known to be composed of at least three sibling species (Webster and Burns, 1973) that remain unnamed. Williams (1977) pointed out the futility of now attempting to answer the basic question "How many species?" in the genus *Anolis*; the answer remains uncertain for a variety of reasons (see also Williams, 1976a), not the least of which are more ready accessibility of some areas and more careful and detailed collecting. The island of Hispaniola demonstrates these phenomena more strongly than any other of the West Indies.

I have summarized elsewhere (Schwartz, 1973) the striking number of new species of *Anolis* described from Hispaniola. As of 1977, 13

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Submitted for publication 8 November 1977.

new species have been described since 1960 as follows: *alumina* Hertz, *barahonae* Williams, *christopheii* Williams, *dolichocephalus* Williams, *fowleri* Schwartz, *insolitus* Williams and Rand, *koopmani* Rand, *marcanoii* Williams, *rimarum* Thomas and Schwartz, *rupinae* Williams and Webster, *sheplani* Schwartz, *singularis* Williams, and *whitemani* Williams. This listing is pertinent in that it includes anoles from a variety of habitats and with a variety of relationships. Six may appropriately be considered siblings of better known species: *alumina*, *barahonae*, *dolichocephalus*, *marcanoii*, *rupinae*, and *whitemani*. Nine may be considered upland or forest-dwelling species: *barahonae*, *christopheii*, *dolichocephalus*, *fowleri*, *insolitus*, *koopmani*, *rupinae*, *sheplani*, and *singularis*. One is an inhabitant of boulder jumbles (*rimarum*) and another of arid lowland desert (*whitemani*). Two are primitive (*insolitus*, *sheplani*). Five are known only from one or a very few localities (*fowleri*, *koopmani*, *rimarum*, *rupinae*, *sheplani*), whereas five are relatively widespread geographically (*alumina*, *dolichocephalus*, *insolitus*, *singularis*, *whitemani*).

The West Indian island of Hispaniola is customarily divided into two major segments, corresponding to the two paleoislands that were separated by a seaway that is now the Cul de Sac-Valle de Neiba plain—the north and south islands. Of the 13 newly named species of *Anolis*, five (*alumina*, *barahonae*, *dolichocephalus*, *koopmani*, *rupinae*) are restricted to the old south island (where none of them is truly widely distributed) and six (*christopheii*, *fowleri*, *insolitus*, *marcanoii*, *rimarum*, *whitemani*) are either restricted to the north island or have the major portion of their distributions there (*whitemani*, the exception, occurs in the Cul de Sac-Valle de Neiba plain but is also broadly, but apparently disjunctly, distributed over xeric areas on the southern and western portions of the north island). Two species are somewhat anomalous—*sheplani* occurs primarily in the south island Sierra de Baoruco but has been taken in the north island Sierra de Neiba, the range that forms the southern border of the north island, and where presumably it is a relatively recent invader, and *singularis* is widespread on the south island but it (or a close relative) occurs in the north island Sierra Martín García, an eastern affiliate of the Sierra de Neiba, and on Ile de la Gonâve. Thus, of the 13 newly named species, seven may appropriately be considered south island in affinities and six are north island lizards.

One niche that Antillean anoles have been unsuccessful in invading is that of streams or rivers. Only on Cuba is there an aquatic anole, *A. vermiculatus* Duméril and Bibron. This species has a relatively limited distribution in the western province of Pinar del Río. In small rivers and creeks, especially those passing through shrubby or wooded situations, *A. vermiculatus* is a relatively common lizard. The presence

of streamside shrubby growth and low trees and saplings are important for *A. vermiculatus*, because it sleeps on these plants. Large rocks and boulders are not necessary for its success, and the lizard may be common along placid streams. *A. vermiculatus* is not limited to only high elevations in Pinar del Río Province but occurs near sea level, provided streams with the proper sleeping sites exist. During the day, when the lizards are disturbed, they plunge into the water and go to the bottom where their cryptic browns and dull blues and greens act as almost perfect camouflage.

Elsewhere, on the Central and South American mainland, there are five species that are stream-associated—*barkeri* Schmidt, *aquaticus* Taylor, *lionotus* Cope, *poecilopus* Cope, and *macrolepis* Boulenger. These species extend from southern México (Oaxaca and Veracruz) to Colombia. Habits and habitat, as well as some meristic data for these species can be found in Taylor (1956), Robinson (1962), Meyer (1968), and Campbell (1973). The latter author gives a comprehensive summary of the literature on the mainland species (except *A. macrolepis*).

Thus, a total of six species of the huge genus *Anolis* are known to have been successful in occupying a niche that appears to be broadly open throughout much of the range of the genus. As Williams (1976a; 1977) pointed out, mainland anoles are much less well known than those of the West Indies, so it is likely that additional aquatic anoles will be found on the mainland. If these mainland species are restricted geographically or altitudinally, then it will be mere chance that they are discovered. Although the Antilles have been known to have a single aquatic species in Cuba, it seemed very unlikely that there might be another aquatic anole on these islands.

On 2 August 1977, while returning from Carrefour Marmelade and on the main road between Plaisance and Limbé in the western portion of the Massif du Nord in northern Haiti, Eugene D. Graham, Jr., Thomas M. Thurmond, and I stopped at a boulder-strewn stream in the late afternoon (about 1630 h). Our objective was to look over the stream as a prospective place for night-collecting of frogs. The stream, in an open ravine perhaps 6 m wide, is at a place known locally as Roche Parfait; although one might not appropriately consider this a torrential stream, still it rushes down a steep slope. Its banks and the stream bed are littered with boulders and rocks of various sizes, some as large as 2 or 3 m or even larger in diameter (see Fig. 1). The newly constructed road, at this point, did not utilize the old road with its culvert and bridge, so that there is, just to the west of the main road, a U-shaped curve with a culvert. The new road has a larger culvert, and the stream then proceeds down a steep slope to the Rivière du Limbé below. The area is remarkable for two reasons—there are no

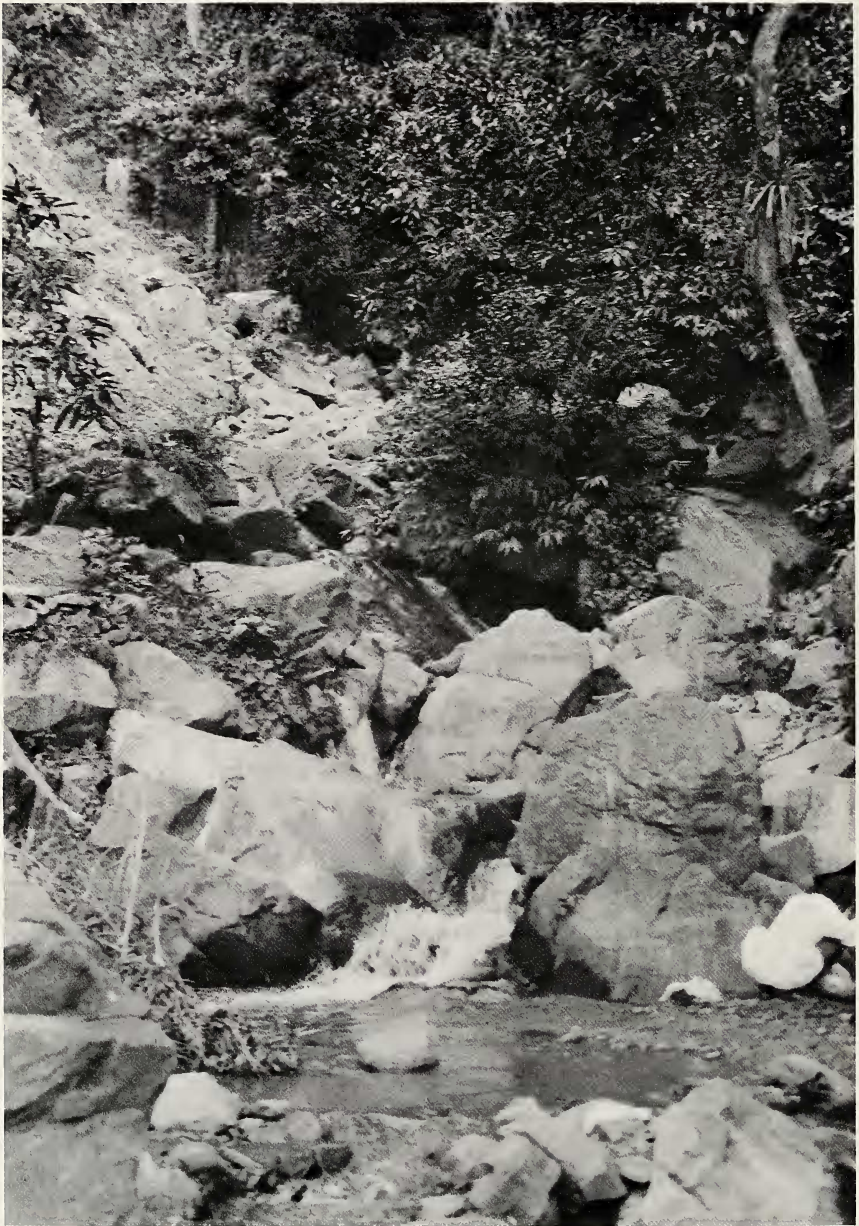


Fig. 1.—View of the type-locality of *Anolis eugenegrahami*, from a Kodachrome transparency by Eugene D. Graham, Jr. The view is from the vicinity of the old culvert upstream, and the waterfall can be seen in the upper left.

human inhabitants in the immediate vicinity of the stream, and there is relatively luxuriant gallery forest, with bromeliads, ferns, shrubs, mosses, and lichens. Because so many streams in Haiti have houses adjacent to them and have had most of their gallery forest removed, this particular stream seemed exceptionally intriguing for frog collecting.

Graham and Thurmond ascended the stream as far as they were conveniently able. About 305 (linear) m above the road, there is a vertical waterfall ending in a shallow pool. An almost vertical path ascends the slope adjacent to the waterfall, but they did not (nor did we later) ascend this path. Upon returning to the automobile, they commented that they had seen many very dark anoles on the bank of the pool at the foot of the waterfall and on the boulders in the stream. When disturbed, the lizards sought refuge under wet boulders in the stream and in indentations behind the waterfall, never outside the stream margins. The lizards were very active on the rocks. One male was seen on a log fallen into the stream; this individual jumped off the log and scurried upstream on the rocks. I asked them whether these dark anoles might be one of the three abundant and widespread north island species—*A. cybotes* Cope, *A. distichus* Cope, or *A. chlorocyanus* Duméril and Bibron. None of these is “normally” black or seeks refuge in aquatic situations. However, despite the fact that *A. chlorocyanus* is customarily bright green, it does show a very dark brown to almost black phase. Because it is a shade-dwelling species, and the ravine is shaded, *A. chlorocyanus* seemed the most likely candidate for the lizards Graham and Thurmond had seen. The situation was equivocal but remained temporarily unresolved.

On the night of 4 August 1977, between 2200 and 2400 h, we visited the stream to collect frogs. We had already been collecting since 1930 h near Carrefour Marmelade in the uplands of the Massif du Nord and were on our way to Cap-Haïtien, when we decided to try for frogs in the Roche Parfait stream. Within 30 m of the old culvert, I stopped to relax in midstream for a minute or two against a large boulder. I felt something alive underneath my shirt and involuntarily brushed at it and then proceeded upstream. Immediately around the sharp corner of the boulder against which I had rested, I saw a large dark sleeping anole which was unfamiliar, and collected it.

With the knowledge that we had discovered a new anole, we concentrated on securing additional specimens and succeeded in finding 16. The lizards were not uncommon and were easily seen from about 10 m above the old culvert as far as the waterfall. On a second visit on 5 August, we found seven more, all associated with the stream and its boulders (although see comments below). Thus, a total of 23 specimens (10 males, 13 females), both adults and juveniles, of this new

species are available for study. In honor of one of the co-discoverers of this new species, I take very great pleasure in naming and describing it.

DESCRIPTION

Anolis eugenegrahami, new species

Holotype.—Carnegie Museum (CM) 60515, an adult male, from Roche Parfait, 9.0 km NE Plaisance, 215 m, Département du Nord, Haiti, one of a series collected on 4 August 1977, by Eugene D. Graham, Jr., Albert Schwartz, and Thomas M. Thurmond. Original number Albert Schwartz Field Series (ASFS) V45823.

Paratypes.—ASFS V45840-46, same locality and collectors as holotype, 5 August 1977; American Museum of Natural History (AMNH) 115515-16, CM 60516-18, Museum of Comparative Zoology (MCZ) 132384-87, National Museum of Natural History (USNM) 197326-29, same data as holotype.

Definition.—An aquatic species of *Anolis* characterized by the following combination of characters: size moderate (males to 72 mm, females to 61 mm snout-vent lengths); moderately sexually dichromatic, males black to greenish black dorsally, females black but mottled greenish laterally and with a middorsal series of four gray ovate blotches extending onto the dorsal side of the yellowish green tail; dewlap in males relatively small, black to dark gray centrally, edged whitish to very pale yellow; a narrow pale yellowish subocular semicircle; nape pattern (clearest in females and juveniles, much obscured in males) of a dark-edged hollow "collar;" upper surface of head randomly vermiculate with black on an olive to gray ground; juveniles with a green flank stripe, absent in adults of both sexes; snout scales at level of second canthal scale 12 to 15; scales between supraorbital semicircles two to four; scales between supraorbital semicircles and interparietal scale tiny, from six to 10; 13 to 18 scales around small interparietal; four to eight postrostral scales; dorsal scales tiny, with about four middorsal longitudinal rows elongate and smooth to very weakly keeled, all other dorsal scales tiny and almost granular, 40 to 56 middorsals in snout-ear distance; ventral scales small, smooth, 37 to 63 in snout-ear distance; canthal scales three to six, with the most anterior ones not larger than adjacent scales; always one row of scales between the subocular scales and the supralabial scales; five to seven postmental scales; femur length/snout-vent length ratio 30.1 to 32.2 in males, 28.6 to 32.3 in females (all sizes combined).

Distribution.—Known only from the type-locality.

Description of the holotype.—An adult male with a snout-vent length of 72 mm and tail length of about 130 mm, distal half regenerated; snout scales at level of second canthal scales 12, six rows of loreal scales, supraorbital semicircles separated by three rows of scales, eight scales on each side between the interparietal scale and the su-

praorbital semicircles, 16 tiny scales around interparietal scale, about 11 enlarged scales in supraocular disk, median dorsal scales in snout-anterior border of ear distance 44, ventrals in snout-ear distance 48, supralabial scales separated from subocular scales by two rows of scales, six postmental scales, six scales in posterior contact with the rostral scales, five and four enlarged canthal scales on right and left sides of head, respectively; subdigital lamellae on phalanges II and III of fourth toe 26; femur length (taken as proposed by Ruibal and Williams, 1961) 22.4 mm; femur/snout-vent length ratio ($\times 100$) 31.1. Coloration in life: dorsal ground color black; head and nape olive with random black vermiculations; a narrow subocular yellowish semicircle; ventral ground color black, mottled with whitish; dewlap black centrally, edged with whitish; tail very dull gray-green to gray.

Variation

The series consists of 10 males (ranging from three adults with snout-vent lengths of 72 mm to a juvenile with a snout-vent length of 35 mm; males are easily distinguished because they possess a pair of enlarged postanal scales), and 13 females with snout-vent lengths of 61 mm to 29 mm. Scutellar variation may be summarized as follows (see also Table 1); I follow the schema used by Williams and Rand (1969).

Head.—Short, moderately broad posteriorly, the appearance being distinctly short-nosed. Head scales small to tiny, smooth to weakly striate in both sexes, smallest on occiput; 12 to 15 ($M_0 = 12$; mean = 12.4) scales across snout at level of second canthal scales; enlarged canthal scales three to six ($M_0 = 5/5$; the fractional designation used here and elsewhere denotes the counts on both sides of the head), the broad variation in this count being due to the relatively abrupt shortening of the most anterior canthal scales so that they become indistinguishable from adjacent snout-scales, counts ranging from 3/3 to 5/6 in the entire series. Nostril longitudinally oval; nasal scale in contact with rostral scale. Rostral scale short and low, about 2.5 times as wide as high, in contact with 4 to 8 ($M_0 = 6$; mean = 6.1) scales posteriorly (not counting nasal scales).

Supraorbital semicircles rather small, more or less parallel for the anterior halves, scales uncarinate laterally, the keels low in both sexes, separated by two to four ($M_0 = 3$) rows of small scales. A very distinct row of supraciliary scales, of which the anterior three are larger and almost shelflike, and more distinct than the much smaller posterior ones, the second (counting from the anterior) the most elongate. Posterior and medially to the supraciliary row, about five irregular rows of small scales that blend almost imperceptibly into the enlarged scales of the supraocular disk, which has about six to 13 enlarged uncarinate scales, the gradation between the disk scales and surrounding scales making decisions as to what is an "enlarged scale" extremely difficult. Loreal rows five to seven ($M_0 = 5$; mean = 6.3), regularly arranged and generally rectangular or polygonal in shape. Temporal scales very tiny and granular, about 25 between the enlarged postocular scales and external auditory meatus. Interparietal scale not lying in a distinct depression in either sex, surrounded by 13 to 18 (mean = 15.8) small smooth scales. Interparietal very small, about one-third to one-quarter the size of the external auditory meatus; interparietal separated from supraorbital semicircles by six to 10 small scales (combinations include 6/6, 7/7, 7/8, 8/8, 9/9, 9/10, 7/9, 8/10; the first three categories with 5 individuals each). External auditory meatus relatively small, about 30 times as large as the largest bordering temporal scale, ventrally placed, and slightly above the level of the oral commissure.

Subocular scales always separated from supralabial scales by one row of scales, anteriorly grading into the loreal scales and posteriorly grading rapidly into the tiny temporals. Seven or eight supralabials to center of eye.

Mental scale large, semidivided, wider than deep, in contact with five to seven ($M_0 = 6$; mean = 5.9) postmental scales; one sublabial and one infralabial in contact with mental on each side. Throat scales elongate anteriorly, becoming increasingly smaller and circular to subcircular posteriorly.

Table 1.—Data for seven species of aquatic anoles. Characters given are: 1) largest male and female; 2) snout scales between second canthals; 3) vertical loreal rows; 4) scales between supraorbital semicircles; 5) scales between semicircles and interparietal; 6) scales around interparietal; 7) scales in supraorbital disk; 8) poststrals; 9) postmentals; 10) dorsal scales in one head length; 11) ventral scales in one head length; 12) canthals; 13) fourth toe lamellae II + III; 14) scale rows between suboculars and supra-labials; 15) ratio femur length/snout-vent length.

Data on *A. barkeri* published by Meyer (1968) modify some data given here. The lowest interparietal scale count (character 6) and lowest femur/snout-vent length ratio in males (character 15) in *Anolis poeciloopus* are both from a specimen (MCZ 139348) that may be misidentified. The next-lowest value for scales around the interparietal is 17 (from KU 75964), and for femur length/snout-vent length ratio is 28.2 (KU 75966).

Charac- ter	<i>Anolis</i> <i>eugenebradami</i> (N = 25)	<i>Anolis</i> <i>vermiculatus</i> (N = 15)	<i>Anolis</i> <i>barkeri</i> (N = 10)	<i>Anolis</i> <i>ilonotus</i> (N = 28)	<i>Anolis</i> <i>aquatius</i> (N = 19)	<i>Anolis</i> <i>poeciloopus</i> (N = 18)	<i>Anolis</i> <i>macrolepis</i> (N = 20)
1	$\delta = 72$, $\eta = 61$ mean = 12.4 $M_0 = 12$	$\delta = 123$, $\eta = 83$ mean = 9.6 $M_0 = 9/10$	$\delta = 95$, $\eta = 78$ mean = 7.4 $M_0 = 8$	$\delta = 73$, $\eta = 67$ mean = 9.9 $M_0 = 9$	$\delta = 73$, $\eta = 63$ mean = 11.1 $M_0 = 10$	$\delta = 67$, $\eta = 66$ mean = 17.4 $M_0 = 16/18$	$\delta = 62$, $\eta = 55$ mean = 8.9 $M_0 = 9$
2	12-15	8-11	6-9	7-14	8-16	15-20	8-10
3	5-7	9-11	7-12	7-13	9-12	8-13	6-9
	mean = 6.3 $M_0 = 6$	mean = 9.7 $M_0 = 9$	mean = 7.8 $M_0 = 8$	mean = 9.5 $M_0 = 9$	mean = 10.5 $M_0 = 10$	mean = 10.1 $M_0 = 9/11$	mean = 7.1 $M_0 = 6$
4	2 (9), 3 (13), 4 (1)	1 (1), 2 (12), 3 (2)	1 (8), 2 (2)	0 (5), 1 (10), 2 (12), 3 (1)	2 (3), 3 (7), 4 (9)	3 (5), 4 (13)	0 (10), 1 (10)
5	6/6 (5), 7/8 (5), 8/8 (4), 9/9 (1), 9/10 (1), 7/9 (1), 8/10 (1)	3/3 (1), 3/4 (1), 4/4 (6), 4/5 (3), 5/5 (2), 6/6 (1)	3/3 (1), 4/4 (5), 4/5 (2), 5/5 (1), 6/6 (1)	0/0 (1), 0/1 (1), 1/1 (12), 1/2 (8), 2/2 (5), 2/3 (1)	4/4 (1), 4/5 (1), 5/5 (1), 5/6 (2), 6/6 (1), 7/7 (5), 7/8 (1), 8/8 (1), 9/9 (2), 9/10 (1), 10/11 (1), 6/9 (1), 7/9 (1)	2/2 (1), 3/3 (2), 3/4 (1), 4/4 (4), 4/5 (2), 5/5 (2), 5/6 (1), 6/6 (2), 7/8 (1), 4/6 (1), 5/7 (1)	0/0 (5), 0/1 (4), 1/1 (11)
6	13-18	15-24	9-14	8-15	8-26	9-25	12-19
	mean = 15.8	mean = 19.3	mean = 11.1	mean = 11.4	mean = 17.3	mean = 20.7	mean = 14.8

Table 1.—(Continued)

Char- acter	<i>Anolis</i> <i>eugenegrahami</i> (N = 23)	<i>Anolis</i> <i>vermiculatus</i> (N = 15)	<i>Anolis</i> <i>barkeri</i> (N = 10)	<i>Anolis</i> <i>lionotus</i> (N = 28)	<i>Anolis</i> <i>aquaticus</i> (N = 19)	<i>Anolis</i> <i>poecitopus</i> (N = 18)	<i>Anolis</i> <i>macrolepis</i> (N = 20)
7	6-13 mean = 8.3	7-16 mean = 11.3	6-12 mean = 8.7	2-10 mean = 5.1	10-23 mean = 16.1	7-15 mean = 11.1	3-6 mean = 4.4
8	4-8 mean = 6.1 M ₀ = 6	7-11 mean = 9.1 M ₀ = 9	3-10 mean = 7.1 M ₀ = 8	6-10 mean = 7.8 M ₀ = 8	8-11 mean = 9.3 M ₀ = 9/10	6-9 mean = 7.7 M ₀ = 8	6-9 mean = 8.1 M ₀ = 7
9	5-7 mean = 5.9 M ₀ = 6	4-8 mean = 5.9 M ₀ = 6	4-6 mean = 5.1 M ₀ = 6	5-10 mean = 7.1 M ₀ = 6	4-11 mean = 8.3 M ₀ = 10	6-8 mean = 6.7 M ₀ = 6	4-7 mean = 5.7 M ₀ = 6
10	40-56 mean = 46.0	50-63 mean = 55.8	36-43 mean = 39.8	21-38 mean = 29.5	33-52 mean = 40.8	30-49 mean = 39.7	19-27 mean = 22.1
11	37-63 mean = 49.5	45-61 mean = 52.6	33-52 mean = 45.0	33-55 mean = 41.3	30-44 mean = 36.1	34-52 mean = 41.3	28-45 mean = 37.6
12	3/3 (1), 4/4 (4), 4/5 (3), 5/5 (18), 5/6 (1), 4/6 (1)	4/5 (1), 5/5 (3), 5/6 (2), 6/6 (5), 6/7 (2), 7/7 (1)	4/4 (6), 4/5 (2), 5/5 (2)	3/4 (1), 4/4 (12), 4/5 (15), 5/5 (10)	3/3 (5), 3/4 (1), 4/4 (13)	3/3 (10), 4/4 (7), 5/6 (1)	3/3 (4), 3/4 (3), 4/4 (13)
13	23-29 mean = 25.9	27-31 mean = 29.1	15-18 mean = 16.5	15-18 mean = 16.0	12-17 mean = 15.3	13-19 mean = 16.6	13-17 mean = 15.4
14	1 (46)	1 (28), 2 (1)	0 (14), 1 (5)	0 (9), 1 (47)	1 (2), 2 (36)	0 (7), 1 (27)	0 (13), 1 (27)
15	♂: 30.1-32.2 mean = 31.1 ♀: 28.6-32.3 mean = 31.0	♂: 26.6-30.4 mean = 28.6 ♀: 27.8-31.1 mean = 29.3	♂: 26.3-28.7 mean = 28.2 ♀: 26.4-32.1 mean = 29.7	♂: 27.1-31.7 mean = 26.0 ♀: 26.5-31.1 mean = 28.5	♂: 27.8-31.8 mean = 30.0 ♀: 25.8-38.4 mean = 29.8	♂: 26.6-34.1 mean = 30.9 ♀: 27.1-32.0 mean = 30.3	♂: 29.0-34.5 mean = 31.6 ♀: 27.9-34.0 mean = 31.3

Trunk.—Dorsal scales small, a median zone of slightly larger scales, elongate rectangular and slightly keeled to smooth, 40 to 56 (mean = 46.0) in snout-anterior margin of ear distance, rapidly becoming smaller and granular on back and flanks, and somewhat larger (about four times) ventrally, the ventrals smooth and rounded, not overlapping; no middorsal crest scales; ventrals vaguely arranged in transverse rows, 37 to 63 (mean = 49.5) in snout-ear distance.

Dewlap.—Relatively small, absent in females, not inset or "slotted;" dewlap scales elongate to papillose, slightly larger than throat scales, slightly smaller than middorsal trunk scales; dewlap scales not arranged in well-spaced rows but rather crowded together, those along the free edge of the dewlap even more crowded and keeled; dewlap black to dark gray centrally, free edge whitish to very pale yellow.

Limbs and digits.—Limbs especially long, tibia length in adults about 1.3 times as great as snout-ear distance, hind foot about 1.2 times as long as tibia. Twenty-three to 29 subdigital lamellae under phalanges II and III of fourth toe. All enlarged limb scales uni- (on thigh and crus) or multicarinate (on pes), including supradigital scales. Anterior thigh scales much larger than granular posterior thigh scales and slightly larger than ventral scales.

Tail.—Very slightly compressed to a vertical oval in cross section, length in adults less than twice snout-vent length; middorsal caudal scales enlarged, almost spinose; tail strongly verticillate, with four or five middorsal scales per verticil and four or five uncarinate ventral scales per verticil near base of tail; lateral caudal scales uncarinate, about one-quarter size of ventral caudal scales; about four rows of enlarged ventral caudal scales; scales around base of tail and behind vent smooth and granular, comparable in size to lateral trunk scales.

Hemipenis.—Large, very weakly bilobed apically, the sulcate surface smooth, the nonsulcate surface with about four basal flounces and many small to tiny calyces apically.

Coloration and pattern.—*A. eugenegrahami* is weakly sexually dichromatic. The general appearance of both sexes in life is black or very dark gray. One male was noted as being greenish black. The dewlap in males is black with a white to very pale yellow edge, and there is in both sexes a pale yellowish subocular semicircle. In males, the venter is black to dark gray, mottled with whitish; tails are very dull gray-green to gray. Females are likewise black dorsally; laterally they are mottled with greenish, and there is a middorsal series of four ovate gray blotches (separated by black papilionaceous figures) that extends onto the yellowish green tail. In males, the head is olive green, in females grayish, with random black vermiculations. In females, the neck is olivaceous, and there is a hollow black-edged "collar." In females, the limbs are banded black to dark gray and olive to pale gray; the venter is pale olive to whitish.

Juveniles are like females, only more contrastingly colored; in addition there is a dull green flank stripe, with four black diagonal bars below it. There is a series of three black lines that extend onto the lower lip radiating from the eye and on a gray-green ground. Female (and assumably juvenile) patterns are more prominent during the day than at night, but in no way should these markings and pattern be considered bright. The general aspect of both sexes in life is of a very dark (black) lizard with a minimum of obvious pattern; juveniles are exceptional in that the flank stripe is moderately obvious even at night. The black female and juvenile "collar" is visible but not a striking feature; the same is true of the vermiculate head pattern.

Comparisons

The distinctive features of *A. eugenegrahami* distinguish it at once from all other known species of aquatic anoles. None is basically a black lizard. These species all have compressed tails, whereas the tail in *eugenegrahami* is very weakly compressed. *A. vermiculatus* lacks

a dewlap (and rather has a prominent transverse gular fold), whereas the dewlap colors in the remaining continental species are all bright (reds to oranges; dewlap color unknown in *A. macrolepis*), in contrast to the somber dewlap in *eugenegrahami*. The ventral scales are keeled in the other six species, small and virtually granular in *eugenegrahami*. Of these seven species, male *vermiculatus* are the largest (123 mm snout-vent length), *barkeri* ranks second (101 mm), and the remaining five species are about the same size (maximum sizes 62 to 76 mm in males).

Meristic data for the seven known aquatic species of *Anolis* are given in Table 1. I have made no effort to examine long series of those species other than *A. eugenegrahami*, and in one case (*A. barkeri*) published data expand the parameters of some scale counts. Nevertheless, the comparative data show the differences between the seven species and emphasize the differences between them and *A. eugenegrahami*. According to the Etheridge (1960) system, *A. vermiculatus* is an Alpha section anole and the remaining mainland species belong to the Beta section.

A. eugenegrahami has a mean of 12.4 snout scales between the second canthals; all other species with the exception of *A. poecilopus* (mean = 17.4) have lesser means (7.4 to 11.1). *A. eugenegrahami* has fewer loreal rows (mean = 6.3) than any other species (7.1 to 10.5). The modal number of scales between the supraorbital semicircles is one (*barkeri*), two (*vermiculatus*, *lionotus*), three (*eugenegrahami*), and four (*aquaticus*, *poecilopus*), with *macrolepis* evenly divided between zero and one. Scales between the interparietal and the supraorbital semicircles vary in *A. eugenegrahami* between 6/6 and 9/10 (modes 6/6, 7/7, 7/8—each with five individuals), in *A. vermiculatus* between 3/3 and 6/6 (mode 4/4), in *A. barkeri* between 3/3 and 6/6 (mode 4/4), in *A. lionotus* between 0/0 and 2/3 (mode 1/1), in *A. aquaticus* between 4/4 and 10/11 (mode 7/7), in *A. poecilopus* between 2/2 and 7/8 (mode 4/4), and in *A. macrolepis* between 0/0 and 1/1 (mode 1/1). The extreme variation in this character in *A. eugenegrahami*, *A. aquaticus*, and *A. poecilopus* is noteworthy. *A. eugenegrahami*, with a mean of 15.8, stands about midway in the series in number of scales around the interparietal (means of 11.1 in *A. barkeri*, 20.7 in *A. poecilopus*).

A. eugenegrahami has the lowest mean number (6.1) of postrostrals of the entire series; *A. barkeri* is next highest (7.1) and the highest is *A. aquaticus* (9.3); there is virtually no overlap in this count between *A. eugenegrahami* (four to eight) and *A. aquaticus* (eight to 11). As far as postmentals are concerned, *A. eugenegrahami* has a low mean (5.9), but those of *A. barkeri* (5.1) and *A. macrolepis* (5.7) are even lower; the high mean is that of *A. aquaticus* (8.3). The smallest dorsal scales are those of *A. vermiculatus* (mean = 55.8), the largest those

of *A. macrolepis* (mean = 22.1); *A. eugenegrahami* stands near the upper extreme (mean = 46.0). The smallest ventral scales are those of *A. vermiculatus* (mean = 52.6), the largest *A. aquaticus* (mean = 36.1); *A. eugenegrahami* stands near the upper extreme (mean = 49.5). Enlarged canthal scales in the entire series of species vary between 3/3 (*A. eugenegrahami*, *A. aquaticus*, and *A. poecilopus*) and 7/7 (*A. vermiculatus*). Modes are 3/3 (*A. poecilopus*), 4/4 (*A. barkeri*, *A. aquaticus*, *A. macrolepis*), 5/5 (*A. eugenegrahami*), and 6/6 (*A. vermiculatus*); *A. lionotus* has an anomalous mode of 4/5 (15 individuals), with incidences of 12 for 4/4 and 10 for 5/5. The two Antillean species, *A. eugenegrahami* and *A. vermiculatus*, have high fourth toe lamellae counts—23 to 29 in the former, 27 to 31 in the latter; these counts in the mainland species vary between 12 (*A. aquaticus*) and 19 (*A. poecilopus*). The scales between the subocular scales and the supralabials vary in the entire series from zero to two. A mode of zero occurs in *A. barkeri*, of one in *A. eugenegrahami*, *A. vermiculatus*, *A. lionotus*, *A. poecilopus*, and *A. macrolepis*, and of two in *A. aquaticus*. The highest mean femur length/snout-vent length ratio in each sex, all sizes combined, is that of *A. macrolepis* (males 31.6, females 31.3), with *A. eugenegrahami* second (males 31.1, females 31.0), and *A. lionotus* lowest (males 26.0, females 28.5). The extreme ratios in males vary between 26.3 (*A. barkeri*) and 34.5 (*A. macrolepis*), in females between 25.8 and 38.4 (both in *A. aquaticus*).

There is no need to compare *A. eugenegrahami* with any other Hispaniolan (or indeed Antillean) anole. Except for *A. vermiculatus*, none is aquatic; *A. eugenegrahami* is eminently distinct from that Cuban species. Both species are Alpha section *Anolis* according to the Etheridge (1960) schema, but *A. vermiculatus* belongs to a different series—the *lucius* series with four members, all of which are Cuban (see Williams, 1976b:14). No other Hispaniolan anole has a black dewlap with a white edge; although black is involved with the dewlap of *A. chlorocyanus*, the dewlap there is vertically bicolored, with the anterior portion pale blue and the posterior portion inky blue to black. The dewlap color, somber hues, and subdued pattern, as well as the habitat, all immediately distinguish *A. eugenegrahami* from all Antillean congeners. Pertinent comparisons with mainland aquatic species have been made above; once again, *A. eugenegrahami* is shown to be quite distinctive.

That *A. eugenegrahami* is unique from all other Hispaniolan anoles as well as from all other aquatic anoles is unquestioned. However, a troublesome fact remained; the species is so very different in such a variety of morphological (and ethological) characters that one is left without any obvious and certain Antillean relatives with which to associate it.

Ernest E. Williams was equally puzzled as to the affinities of *A. eugenegrahami*, and he, with the competent assistance of Susan Rhodin, made skeletal preparations of two of the MCZ paratypes. His amazement at the results is equal to my own. *A. eugenegrahami* is an Alpha section anole (as expected) belonging to Etheridge's (1960) *bimaculatus* group, a group which on Hispaniola is otherwise represented only by the distichoid anoles (*A. distichus* Cope and *A. brevirostris* Bocourt and its allies). Williams (*in litt.*, 3 October 1977) stated that *A. eugenegrahami* is so assigned because it has "caudal vertebrae without transverse processes, lateral processes of the interclavicle divergent from the proximal parts of the clavicles, lower jaw smooth (i.e. without sculpturing present in some members of the *crisatellus* group). Splenial present. Pineal foramen at the fronto-parietal suture as a U-shaped notch on the parietal. Inscriptional rib formula 3:1 (3 attached, one free). The one feature in which *A. eugenegrahami* differs from Etheridge's 1960 description of the *bimaculatus* group is the size of the splenial. It is well developed as in *A. richardi*, . . . not small or absent as in previously known members of the group."

Williams's interpretation, following his own (1976*b*) excellent outline of the interrelationships of the Antillean anoles, is that he "would regard *eugenegrahami* as primitive on the basis of the large splenial . . . and would place it in the *bimaculatus* series as its own subseries and species group, placing it, as more primitive, ahead of the *stratulus* subseries, which includes the *evermanni*, *stratulus*, and *distichus* species groups. It may have been an early invader of Hispaniola from Puerto Rico, since the current hypothesis is that the *bimaculatus* series arose in Puerto Rico. The distichoids are undoubtedly late invaders of Hispaniola; this is to be inferred since they are a highly derived group originating from some pre-*stratulus* stock, and *stratulus* itself is highly derived."

I agree wholeheartedly with Williams' (*in litt.*) closing paragraph: "The discovery of this species is exciting beyond the ordinary. Not only is its ecology highly special but it is an apparent relict of a stock primitive for the *bimaculatus* series. It confirms our joint belief that the period of discovery and even of important biogeographic discovery is not yet ended in the West Indies." If I were to make one slight change in Williams's statement, it is that I would change "belief" to either "certainty" or "absolute conviction."

Remarks

I have already discussed in some detail the situation at the type-locality of *A. eugenegrahami*. The site is shown in Fig. 1. Some other observations are pertinent.

On our first nocturnal visit (4 August 1977; 2200 to 2400 h), we

encountered all specimens but one on rock faces. These were almost invariably dry faces; one individual was taken on a wet rock face (but not with water running over it). Most individuals were exposed on vertical rock faces, with a predilection for edges (where two vertical faces intersect to form a rather sharp edge). One individual was taken sleeping upside down in an open nook beneath a moderate-sized boulder. The exceptional lizard (a female) was taken 15 mm above the water, about 30 mm from the bank, on some hanging skimpy vegetation. All individuals slept soundly and were not easily disturbed either by talking or by light. One juvenile, when disturbed, leaped into a shallow (10 mm) pool and swam to the edge where it rested temporarily, and then "disappeared."

On the night of 5 August 1977, I secured a juvenile sleeping on a shrub, 15 mm above the boulder from which the shrub grew; other juveniles were taken sleeping head-up in vertical dry rock faces, and the single male was secured 1.2 m above the water on the edge of a vertical rock face. There seemed to be no effort made at concealment, because most lizards were in the open, and very obvious. Their dark coloration made them very conspicuous against the gray rocks. One large male is noteworthy in that he slept in an S-curve exposed but within a 10 by 20 mm flat cavity on the vertical rock face. Even this site was not an obvious attempt at concealment. The few lizards found on vegetation at night were likewise obvious, but I have the impression that this is not their normal sleeping site.

On Graham's and Thurmond's first diurnal visit, they noted the concentration of the "black" anoles on the rocks and mudbank at the base of the waterfall. They estimated that they saw 15 to 20 lizards, many of which were at the waterfall. Night collecting did not reveal any concentration (nor indeed any lizards) at this site; rather, the lizards were scattered between the waterfall and the old road culvert in a random manner—some widely spaced, others close together. We never secured two on the same boulder, unless a juvenile that sought refuge under my shirt and the sleeping male collected immediately thereafter were from the same huge boulder.

On 7 August 1977, Graham took photographs of the stream at 0945 h. While climbing the incline he saw a female run into a sandy-bottomed cranny 0.6 m above the water to seek refuge. Another female was 3 m from the water and 3.7 m high on a large rock. As noted previously, Graham and Thurmond both observed adults escaping under wet rocks and boulders and into rocky indentations behind the waterfall.

The type-locality is unique in this area. The new Ennery-to-Cap-Haïtien road leaves Ennery to ascend a major spur of the Massif du Nord, the Chaîne de Marmelade, which it crosses at Carrefour Mar-

melade (where a road goes to the east to the town of Marmelade) at 920 m, and then descends into the Plaisance valley (which lies at an elevation of about 305 m). From the town of Plaisance, the road ascends a low (280 m) minor spur of the Massif du Nord (the Morne Lafleur), and then descends to parallel the Rivière du Limbé in its valley to the town of Limbé, which is close to sea level. The type-locality lies on the northern slope of this Plaisance-Limbé montane spur. The elevation is not excessive (215 m), but the combination of a steep and boulder-strewn stream with remnant gallery forest is unique. In an attempt to find other localities for *A. eugenegrahami*, we next collected in an adjacent (but much smaller and narrower) stream without success. Two other streams at the same approximate elevation cross another road between Plaisance and Pilate, a few kilometers northwest of the former town. We visited both of these streams during the day; they are slow-moving and placid, due primarily, we assumed, to the fact that at that point in their courses they are in the flood plain of Les Trois Rivières and about to empty into that major stream.

The Plaisance valley is an enclosed, relatively high, valley; its southern and eastern margins are formed by the Massif du Nord itself, its western and northern margins by a series of small ranges (Morne Lafleur, Morne Crête Rouge, Morne Gris Mango), and finally, to the extreme east, the Morne Bonnet à l'Evêque, the latter merging to the south once more with the Chaîne de Marmelade. From the vantage of Carrefour Marmelade, one looks to the north and is impressed with the lushness of the Plaisance valley, its apparent enclosure, and the jumble of major and minor montane masses and massifs between the valley and the coast to the north and northwest. Although I feel certain that *A. eugenegrahami* is not limited to the Plaisance area (namely, in streams that drain the Morne Lafleur), other immediately adjacent regions have revealed nothing. The most likely area, the northern slopes of the Chaîne de Marmelade, lacks streams of any size and complexity; the few streams and rivulets where I collected in 1974 did not reveal *A. eugenegrahami*. One area suggests itself for further investigation, partially because it has the "right" sort of stream, but it is at a higher elevation. This is the area between Jonas and Dondon in the Morne Bonnet à l'Evêque. It is of course possible that *A. eugenegrahami* is widespread in these mountains and may even extend to the east as far as the northern slopes of the Cordillera Central in the República Dominicana. Too much of the northern slopes of the Massif du Nord is simply inaccessible today to make any generalizations about the range of this aquatic lizard.

I have one further comment. Every herpetologist or biological collector who has traveled from Port-au-Prince to Cap-Haïtien on the

north-south road has passed the type-locality of *A. eugenegrahami*. I myself did so many times in 1974. But the road has been in such terrible disrepair that one's attention was directed to it rather than to the surrounding countryside. In 1974, I was unaware of the beauty of this northern portion of Haiti; it is lush and mesic, despite the near absence of original forest cover (although some of that remains as shade trees in *caféières*). My whole impression of northern Haiti is now different, due primarily to the fact that one can now make this formerly arduous, and often hazardous, drive in a relaxed and observant state. That we stopped at Roche Parfait was chance; that Graham and Thurmond climbed the stream bed was due to their industry; that they observed a "black" anole there was a fluke. It is through such sequences of non-biological events that biological discoveries will continue to be made in the West Indies.

DISCUSSION

Antillean anoles come in two general "styles." Because the dewlap serves a dual function—that of territorial declaration and as a sexual recognition device between the two sexes of the same species—it is usually contrastingly and brightly colored in contradistinction to a less brightly colored or more drab body color and pattern (body colors are usually greens, tans, browns, and patterns are unicolor, lineate, spotted, or composed of chevrons or diamonds—the latter in females). This arrangement of a bright or contrasting dewlap and a relatively subdued body pattern is typical of most Antillean anoles. At the other extreme, the dewlap may be very reduced or absent; in such cases the body coloration and pattern are vivid, often gaudy, and complexly colored and patterned; the *hendersoni* group of Hispaniolan anoles is a prime example of this. *Anolis monticola* Shreve is another Hispaniolan example. Thus, to "compensate" for lack of, or reduced, dewlap, sexual recognition and territorial declaration at least must depend upon the distinctive and brightly colored body pattern.

A. eugenegrahami does not readily fall into either of these styles. The body colors are dull, somber, and dark; even the more clearly marked females are not to be construed as being vividly colored or patterned. Thus, one might reasonably expect that the male dewlap would be brightly colored, but such is not the case because the dewlap is black or dark gray with a white to pale yellow edge and is relatively small for the size of the lizard. It would thus seem that *A. eugenegrahami* contradicts what has been generally supposed to be a "rule" in body pattern-dewlap size and color correlation within anoles. It is intriguing also that the Cuban aquatic *A. vermiculatus* lacks a dewlap and has the body variegated with browns, bluish greens, and greens, once again not especially bright colors and with a random camouflage pattern.

One possible explanation may be that *A. eugenegrahami* occupies such a specialized niche that it has no competitors. Although we observed sleeping *A. cybotes* along the ravine (always on shrubs adjacent to the water, never on rocks), I feel sure that *A. distichus* and *A. chlorocyanus* are likewise present, along with the giant *A. ricordi* Duméril and Bibron in the crowns of the trees. Of these four species, *A. ricordi* is much larger in snout-vent length (males to 160 mm), rarely comes to the ground, and surely never sleeps on rocks or carries on its diurnal activities immediately associated with streams and their beds. It is a brightly colored (green) lizard with a large peach colored dewlap. *A. distichus* is also an arboreal anole; it does, however, venture close to the ground on tree trunks and shrubs and may even be seen on ground litter and rocks. It is mottled greenish, small (local subspecies snout-vent length 58 mm in males), with a pale yellowish to yellowish with an orange central blush dewlap. *A. cybotes* is a stocky tree- and shrub-dwelling anole, but it is not averse to foraging or sunning on rock and cliff faces. The dewlap is very pale yellow to white in northern Haiti. *A. chlorocyanus* is vivid green and long-snouted with a relatively small bicolor dewlap; adult males are slightly smaller in snout-vent length than *A. eugenegrahami*. It is an arboreal anole, seldom coming to the ground to forage. Although it may occur on low shrubs, I have never seen it in strictly terrestrial situations. Thus, the two species with which *A. eugenegrahami* might be most closely associated ecologically and behaviorly are *A. cybotes* and *A. distichus*. The former is much stockier, has a large pale dewlap, and has a pale tan to reddish tan ground color with a greenish lateral stripe. *A. distichus* is smaller, mottled green in color, and has a moderate sized pale dewlap. It would be very difficult indeed for either of this duo of anoles to become confused, if and when they come in contact directly either as far as territory or sex is concerned, with *A. eugenegrahami*, or vice versa. The latter species bears little total resemblance to either *A. cybotes* or *A. distichus* in size, body shape, or habits.

There remain, then, the drab coloration and small dewlaps of *A. eugenegrahami*. The former may possibly be explained as an ecological-camouflage effect—inhabiting well-shaded ravines without any other close competitors, *A. eugenegrahami* may well have evolved a drab pattern to conform to the darkness of its habitat. It does not need to be brightly or contrastingly colored to declare its identity, because no other anoles are likely to occur precisely syntopically with it. The small and black dewlap may be interpreted similarly, that is, in shaded and dull ravines, without competitors, an elaborate and bright dewlap is unnecessary. The most likely candidate that a male *A. eugenegrahami* will encounter for mating is a female *A. eugenegrahami*—this is the only species with such specialized habitat and ecological requirements. If the dewlap is used for territorial declaration in this species

(and there is a possibility that it is not), its display may well be correlated with posturing that enhances the effect of the somber coloration and small dewlap. In the gloom of such a shaded ravine, the pale dewlap *edge* might be more striking than the dark dewlap itself. The comments of Williams and Rand (1977) on multiple-anole faunas are indeed pertinent in the context of *A. eugenegrahami*.

Richard Thomas has pointed out to me that the primitive anoline *Chamaelinorops barbouri* Schmidt, which is also Hispaniolan, has a similarly patterned dewlap; in this case the dewlap is basally dark brownish black with a whitish-to-cream colored edge. *C. barbouri* is a mesic forest anoline and typically is encountered in very shaded situations. The similarity of dewlap pattern (but not particularly coloration) may well be a response to the dull and shaded situation in which both it and *A. eugenegrahami* exist. The body color of *C. barbouri* is basically dark brown, at times with a greenish tinge. Thus, both body and basal dewlap are difficult to distinguish in the gloom of mesic forests; this would seem to make the brighter dewlap edge all the more contrasting and conspicuous when the dewlap is erected.

It would be exceptionally neat if we could state that the dark coloration of both sexes of *A. eugenegrahami* helps in their nocturnal camouflage while they sleep on boulders. At least at this site, this is not the case because the dark colors contrast sharply with the pale gray rocks; the female pattern, dark at night, is not disruptive. Only the juveniles, with an even more complex pattern than females, are slightly difficult to detect, but they, too, are conspicuous. The dark hues of *A. eugenegrahami* must function best during their diurnal activities.

ACKNOWLEDGMENTS

My primary debt of gratitude is to Eugene D. Graham, Jr., and Thomas M. Thurmond for their competent assistance in the field. I have borrowed comparative material from the following institutions and am grateful to the respective curators for these loans: American Museum of Natural History (AMNH), Richard G. Zweifel and George W. Foley; Museum of Natural History, The University of Kansas (KU), William E. Duellman; Museum of Comparative Zoology, Harvard University (MCZ), Ernest E. Williams; Museum of Zoology, The University of Michigan (UMMZ), Arnold G. Kluge. Jay Cole, Howard W. Campbell, William E. Duellman, and Ernest E. Williams have given freely of information at their disposal or helped with literature. Dr. Williams has most generously offered information from his great store of knowledge on anoles in general, and in this case especially those of the continental mainland. Specimens of *A. vermiculatus*, collected by me and now in the AMNH, were taken under National Science Foundation grants G-3865 and G-6252.

SPECIMENS EXAMINED

Anolis vermiculatus.—CUBA. *Pinar del Río*: San Vicente (AMNH 81302—2 specimens; AMNH 81303—4 specimens; AMNH 82304; AMNH 81305—6 specimens); 13.6 km W San Vicente (AMNH 82306); north base, Pan de Azúcar (AMNH 81307).

Anolis barkeri.—MÉXICO. *Oaxaca*: Cerro Azul, La Gloria (MCZ 58221). *Veracruz*,

Río Basura, 4.0 km NW Sontecomapán, Los Tuxtlas (MCZ 92103); between Laguna Catemaco and Volcán Santa Marta (UMMZ 121177–83). *Chiapas*, 4.8 km S Soluschiaipa (MCZ 85008).

Anolis lionotus.—COSTA RICA. *Alajuela*: Cinchona, 488 m (MCZ 92955–64). *Limón*: Madre de Dios (MCZ 129351–54). PANAMÁ. *Colón*: El Valle, 560 m (KU 75952–58). *Coclé*: Achioté, 40 m (KU 75951). *Panamá*: Cerro Campana (KU 127713–14); south slope, Cerro Campana (KU 75948–50).

Anolis aquaticus.—COSTA RICA. *San José*: 15 km SW San Isidro El General, 865 m (MCZ 92902). *Puntarenas*: ca. 1.6 km SE Golfito (MCZ 92901); Rincón de Osa (MCZ 96553, MCZ 110412, MCZ 110571–72, MCZ 109967–69). PANAMÁ. *Chiriquí*: 16 km NE El Volcán, 1,170 m, (KU 107944–49); 9 km NW El Volcán, 1,170 m (KU 107950–52); Finca Ojos de Agua, southeast slope Cerro la Pelota, 1,440 m (KU 107953).

Anolis poecilopus.—PANAMÁ. *Colón*: 3.5 km SE Puerto Pilón, 230 m (KU 113256). *Panamá*: southeast slope, Cerro Jefe, 660–700 m (KU 113251–55, KU 94650). *Canal Zone*: stream near lodge on Pipe Line Road (MCZ 139348). *Darién*: Laguna, 820 m (KU 75962); Tacarcuna, 550 m (KU 75963–69); Quebrada de Taqua, 510 m (KU 75970–71).

Anolis macrolepis.—COLOMBIA. *Chocó*: Río San Juan, Caño Docordo between Currupí and Noanama (MCZ 112317–35). *Condato*: Peña Lisa, 92 m (MCZ 70224).

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